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NOTES ON THE DIVISION OF THE CELL AND NUCLEUS IN LIVERWORTS.

By J. M. VAN HOOK.

(WITH PLATE XXIII)

In the following pages are presented the results of some observations on the division of the cell and nucleus in the spore mother cell of Anthoceros, and in the vegetative cells of the gametophyte of Marchantia.

But little has been done in the cytology of the Hepaticae, aside from a study of the development of spores. Several papers were written by Farmer ('94–'95), whose detailed work has dealt, for the most part, with the cytology of reproductive cells. Along this same line Davis ('99) has worked out spore formation in Anthoceros, and his article upon "The spore mother cell of Anthoceros" strongly suggested the desirability of extending the study.

My observations on Anthoceros confirm his statement concerning the absence of centrospheres, but in regard to the disappearance of the connecting fibers and the formation of the cell plate by the thickening of strands of apparently undifferentiated cytoplasm which extended between the daughter nuclei my own results differ from his.

A cell plate seems to be formed in no wise different from that found in Marchantia, an account of which is given below, *i. e.*, the cell plate is laid down through the instrumentality of the connecting fibers (*figs. 11, 13*). Cytoplasmic strands similar to those figured by Davis are always found between the chloroplasts (*fig. 14*), but are undoubtedly *around* the spindle; and when a section includes only these strands, or if the connecting fibers be insufficiently stained, the appearance figured by him (his *fig. 25*) is presented. The same aspect is also displayed at a later stage, as in his *fig. 26*, but I am inclined to attribute this to the persistence of the protoplasmic strands after the disappearance of the connecting fibers.

In order to see these plates as formed by the thickening of the spindle fibers, it was necessary to cut the sections two or three μ in thickness; for at this stage the daughter nuclei lie very close together, and the protoplasm about them is exceedingly dense. Staining was protracted two or three times the usual length of time, and the excess washed out with great care.

For my study there was placed at my disposal an abundance of excellent material of a species of Anthoceros collected and fixed by Professor Mottier near Naples in April 1898. On account of the large size of the cells and the greater clearness with which the finer details were brought out in the preparations, this material proved to be more favorable than that obtained from the Indiana species, in which many details were brought out with difficulty.

For the behavior of the centrosome in Marchantia we have only the abstract from Mottier ('98). He says: "In the vegetative cells of Marchantia I cannot assert with absolute certainty that a definite central body or centrosome exists in all cases, but I believe that such is the case. In some in which the kinoplasmic radiations are densely stained the dark center seems to be merely the point of union of the radiations, but if the stain be washed out so that the radiations are almost colorless, a well defined and densely stained central body is generally to be seen."

It is further stated that the centrospheres are attached to the nuclear membrane and are almost diametrically opposite by the time the chromosomes are differentiated or even earlier. Farmer's statement that the centrospheres exert a pulling strain upon the nucleus is substantiated. Frequently the nuclear membrane is drawn out by their influence into slender beaks.

For the study of karyokinesis in these vegetative cells the young and rapidly growing stalks of the archegoniophore of Marchantia was selected. These were fixed in the Flemming solution as used by Mottier ('97). A number of stains were used, but the best general results were obtained by the triple method of aniline-safranin, gentian-violet, and orange G. The stains were varied both in kind and length of time of use, in accordance with the structures or parts of the cell which were to be brought out.

The cells from the more rapidly growing stalk of the archegoniophore are in general cubical, and a longitudinal section of the stalk will almost invariably result in meridional sections of the spindles. The resting nuclei are round and contain large conspicuous nucleoli. The nucleolus seems to lie in the cavity or vacuole. A careful examination reveals also a very delicate network of linin threads. These are clearly seen only in successful preparations when sufficiently magnified.

In the granular cytoplasm becoming vacuolate in older cells are situated many oval or rounded chloroplasts, together with metaplasmic inclusions which stain variously. The chloroplasts and metaplasmic inclusions generally collect about the poles of the nuclear spindle, thus obscuring the finer details and rendering observation difficult.

The first noticeable evidence of nuclear division is the pulling out of the nuclear membrane, generally in the direction of the long axis of the cell, into two points which are opposite each other and around which the chloroplasts tend to collect. A careful examination reveals a minute body at each point from which extend conspicuous radiations. These bodies with their radiations are the centrospheres. They seem undoubtedly to exert a great attractive force from the manner in which certain of the cell contents are drawn to them (*figs. 2, 4*). The way in which the nuclear membrane is often drawn out into very long points would seem to indicate further that the centrosphere exerts a pulling force upon it. The exact time of the appearance of the centrosome cannot be stated with certainty, because in the absence of the radiations it is impossible to distinguish the centrosome from other bodies appearing quite like it. From what is known of their behavior in other plants it is reasonable to suppose that they appear before the radiations, for in fact centrosomes can be recognized during the reconstruction of the daughter nucleus after the radiations have disappeared (*fig. 11*). The dense center of the centrosphere, or the centrosome, is best seen previous to the appearance of the mature spindle as a dark round body at the center of many distinct radiations. There is no reason why it should not appear as a temporary body arising from some specialized cytoplasm, as kinoplasm.

As the nucleus increases in length, the radiations become exceedingly distinct and extend farther over the nuclear membrane (*fig. 2*). They also penetrate the nuclear membrane, for any section of the nucleus at this stage will show them in its interior. Before they meet at the middle from the two centrosomes to form the spindle, the linin threads have become more conspicuous with thickened or knotty portions appearing as chromatin (*fig. 3*). This forms a network filling the large central part of the nucleus, but does not seem to extend into the pointed ends. In no case was a continuous band or spirem observed, but a framework of linin at whose crossings or thickened parts chromatin gathers. These increase rapidly in size, separate by the dissolution of the intervening linin, and form a number of chromosomes. The number seems to vary. In one instance I counted five, in another eight. These are irregularly scattered within the nuclear cavity (*fig. 4*). They are often in the form of irregular masses, but sometimes in the shape of straight or bent rods varying in size (*fig. 5*). When arranged in the nuclear plate, however, they are generally U-shaped, and each is seen to be split longitudinally.

The spindle fibers have now extended to the region of the equator, the nuclear membrane disappears, and the spindle is formed. At its center the chromosomes gather, arranging themselves at the circumference of the equatorial plane. The spindle elongates very rapidly. It is pointed, with the centrospheres yet visible at either pole. In many cases it assumes a double curve like an elongated letter S (*fig. 8*). In almost every instance at this stage this curve may be observed. Even those that seem straight may owe their appearance to the manner in which they have been sectioned; and such is undoubtedly the case from the position of the poles and the difficulty in making an exact meridional section. This shape seems to be due to the rapid lengthening of the spindle threads as soon as they have come together at the center. Spindles are often curved, or rather it happens that the poles do not have a common axis. This is observed in their formation, however, and before the centrosomes have taken diametrically opposed positions. The daughter segments separate and pass rapidly toward the poles, along the spindle fibers, which have now become straight. Here they crowd so closely together that they lose their individuality and appear as a broken mass of chromatin, which soon becomes enveloped in a new membrane forming the daughter nuclei (*fig. 9*).

The centrosomes become invisible or perhaps dissolve as soon as the polar radiations have disappeared. The connecting fibers now thicken in the equatorial region, the first indication of a cell plate (*figs. 9, 10*). This thickening begins at the center of the equatorial plane and gradually extends to its circumference, apparently pushing the fibers farther apart toward the cell membrane, until the spindle becomes very much bulged or rounded.

Concomitant with the bulging of the spindle, its connecting fibers begin to shorten and to dissolve at the poles (*fig. 11*). As they disappear toward the cell plate, which finally reaches the membrane, dividing the old cell completely, the daughter nuclei follow, and come to lie very near each other (*fig. 12*).

Thus the process of cell plate formation is almost identical with what I find in Anthoceros. It corresponds also with that described by Mottier ('97) for Lilium.

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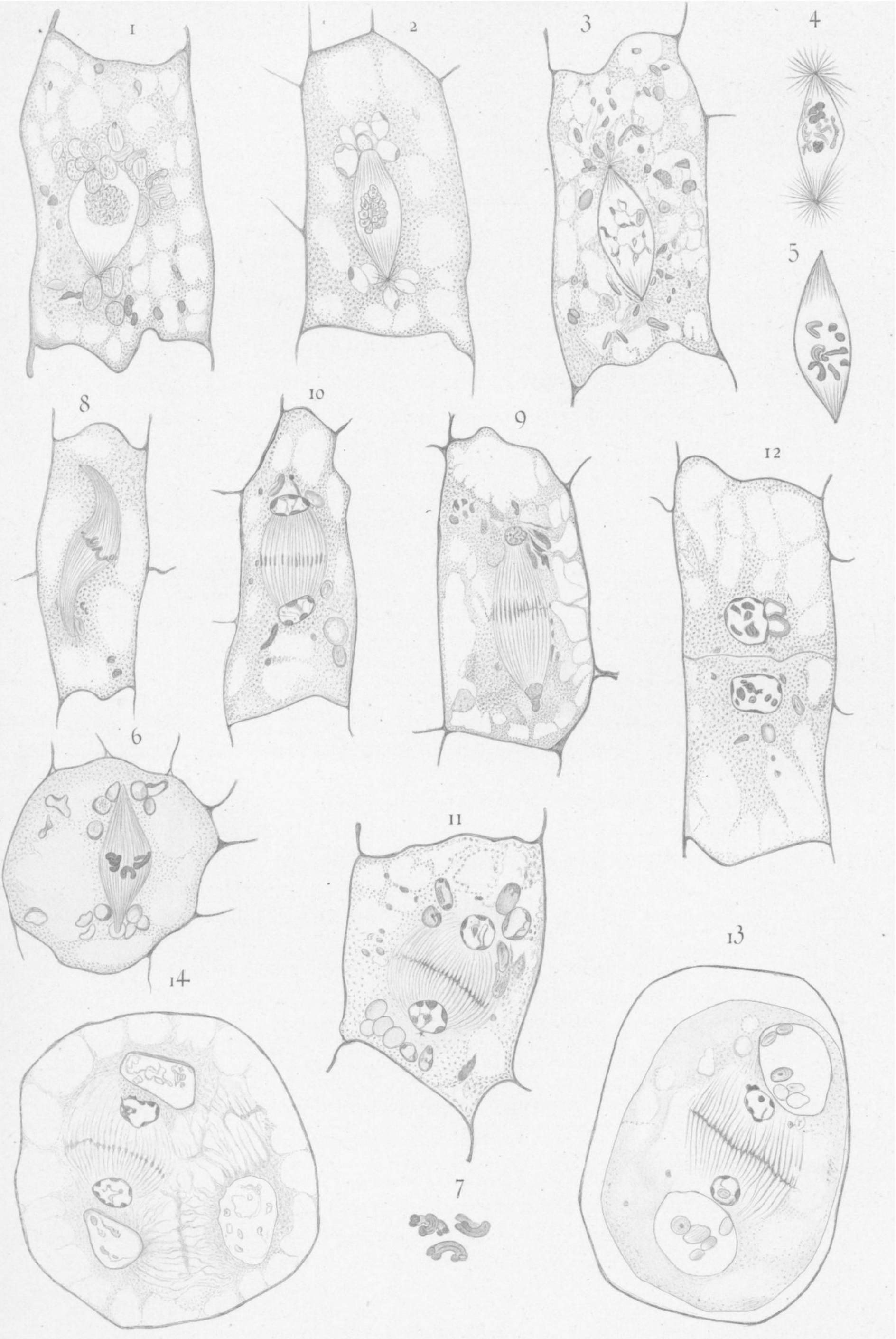

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EXPLANATION OF PLATE XXIII.

The figures were sketched with the aid of an Abbé camera lucida; *figs. 1, 2, 9, 10, 11, 12, 13, 14*, with a Bausch and Lomb $\frac{1}{12}$ oil immersion objective; the others with a Zeiss 2^{mm} oil immersion and compensating ocular 12.

All preparations were fixed in the Flemming solution used by Mottier ('97), and *figs. 11, 13, 14* were from sections 2μ thick; the others, 5μ. All were stained on the slide with Flemming's triple stain of safranin, gentian-violet, and orange G.

FIGS. 1–12, Marchantia; 13–14, Anthoceros.

FIG. 1. Nuclear figure from archegoniophore of Marchantia; the centrospheres are visible.

FIG. 2. The nuclear membrane is drawn out into points, and chloroplasts, with other bodies, are collected about the centrospheres.

FIG. 3. Nucleus previous to formation of the spindle; chromatin masses apparent in the linin net.

FIG. 4. Later stage in which the chromosomes are differentiated.

FIG. 5. Chromosomes collecting in equatorial region.

FIG. 6. Spindle stage with chromosomes arranged in equatorial plane; each chromosome is seen to be split longitudinally.

FIG. 7. Same, more highly magnified.

FIG. 8. A curved spindle.

FIG. 9. Formation of daughter nuclei.

FIG. 10. First appearance of nuclear plate.

FIG. 11. Bulged spindle, plate building toward the cell walls.

FIG. 12. Nuclear plate completed.

FIG. 13. Spore mother cell of Anthoceros, showing two of the nuclei only, and the nuclear plate in process of formation.

FIG. 14. Spore mother cell of Anthoceros, showing two of the nuclei with connecting fibers in which a cell plate is forming; cytoplasmic strands extend also between the chloroplasts and nuclei.